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SHORT CYCLE UROMYCES OF NORTH AMERICA

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(WITH PLATE X)

The short cycle *Uromyces* may be segregated as a group by utilizing the criteria of life cycle and character of teliospores. Aside from any question of the validity of such bases for segregation, it is evident that it is a common practice thus to set apart this group, and that an opportunity is thereby afforded to consider relationships of such rusts to each other and to other rusts.

The short cycle *Uromyces* are of considerable interest, although as yet comparatively few species or even collections are recorded for North America. These rusts occur over a wide geographical range, however, and are parasitic upon widely separated families of hosts.

The writer has been privileged to examine the excellent collection of short cycle *Uromyces* in the herbarium of Dr. J. C. ARTHUR. This paper represents the results of the study of the group as made primarily for the *North American Flora*, but is presented separately in order to give notes and discussions not permissible in that publication.

Abstract submitted before American Phytopathological Society at the New York meeting, and published in Phytopathology 7:74. 1917. Contribution from Botanical Department of Purdue University Agricultural Experiment Station.

Characters and relationships

The rusts considered in this paper are those which fulfil the following requirements:

Cycle of development includes only pycnia (sometimes) and telia, both subepidermal.

Pycnia deep-seated, globose or flask-shaped, with ostiolar filaments.

Telia erumpent, usually grouped; teliospores free, pediceled, 1-celled; wall firm, colored, smooth or variously sculptured; germination by a single promycelium from an apical pore.

Urediniospores normally absent but occasionally found in the telia.

The association of pycnia with telia has for some time been considered the criterion of short cycle rust (1, 4). The occurrence of definite aecia or uredinia (providing the evidence indicates that the aecia or uredinia belong with the telial stage present) suffices to exclude a specimen from the group under consideration. While some suspicion may be aroused by the presence of urediniospores, such spores occasionally occur in the telia. In the cases in which pycnia are only rarely or not at all produced, telia only being present, the arrangement and character of the telia usually may be utilized to indicate whether or not the specimen is short cycled; a grouping of the telia in definite circinating or crowded groups, or the occurrence of germination of the teliospores at or soon after maturity, usually means that such a specimen belongs with the group of rusts here treated. In certain cases, however, the telia are diffused, and other considerations must be brought to bear.

A study of the *Uromyces* forms of the rusts as represented in the Arthur herbarium and of the literature indicates that, in North America, only the 11 species described are at present known to belong in reality to short cycle forms.

DIETEL (10) pointed out that the percentage of endemic species of rusts is higher in proportion to the isolation of the geographical region; that *Uromyces* shows a higher percentage of species in warmer than in colder regions; and that in both the Old and the New World the number of species of *Uromyces* is about one-third that of the number of species of *Puccinia*. It is to be noted that, so far as known, 8 of the 11 short cycle species of *Uromyces* are endemic to North America, and only 1 of the 11 species occurs also in Europe.

These forms are more especially found in the warmer parts of the continent, just as all *Uromyces* seem to be more numerous in warmer regions. While in North America some three times as many species of *Puccinia* as of *Uromyces* exist, the relation of the forms when divided according to their life cycle is strikingly different; for about 140 short cycle species of *Puccinia* are known for North America, in contrast to these 11 species of *Uromyces*.

P. and H. Sydow (25), in their monograph of *Uromyces*, described only the telial stage for 183 of the 504 species considered in that work. For only a very few of these, however, were pycnia described. When full information is in hand, a large number of the 183 forms will of course be found not to be short cycled. It appears, however, that a comparatively greater preponderance of these short cycle forms of *Uromyces* may be found in the more tropical regions. The observation of Magnus (17) and of Fischer (15), that increased altitude results in shortened life cycles for the rusts, is somewhat borne out by the fact that certain short cycle *Uromyces* are limited to the Rocky Mountain region. The effect of altitude and temperature can be better noted with the more numerous short cycle species of *Puccinia*.

ORTON (21) has touched upon the relation of a group of rusts with a common life cycle, opsis forms of Puccinia (the genus Allodus), to other groups with different life cycles. Comparable relationships and correlations with other rusts are to be noted with the group of rusts considered in this paper; some attention is directed to these points with the discussion of the several species. The rust in its development is intimately dependent upon its host. FISCHER (13) in 1898 emphasized the similarity between the teliospores of certain short cycle rusts and of long cycle heteroecious rusts whose aecia occurred upon the host of the short cycle form. He considered that this similarity indicated a phylogenetic relationship between such rusts with different life cycles. Dietel (9) considered that the Uredinales have probably developed during geological times along with their hosts. ARTHUR (5) has pointed out that the relationships of the rusts often reflect the relationships of the hosts upon which they occur. The writer (6) has also dealt somewhat with this point.

DIETEL (II) considered that *Uromyces* is the most primitive of the Pucciniaceae, both on account of the possession of I-celled teliospores, and because it occurs upon such diverse families of monocotyledons and dicotyledons. Whether long cycle or short cycle rusts are more primitive is still a mooted question.

The existence of species of these rusts as lepto-forms or microforms, that is, whether or not the teliospores germinate upon maturity, while subject somewhat to seasonal variation, is a fairly constant and characteristic feature with each species.

Life history; cytology

The life cycle is simplified in a short cycle species to the extent that only telia, often with pycnia, are produced. The occasional occurrence of a few urediniospores in the telia is a phenomenon in common with other groups of rusts which ordinarily do not bear such spores.

Fischer (12) first cultured a short cycle Uromyces. He sowed teliospores of U. Cacaliae (DC.) Unger upon Adenostyles alpina Kern, securing telia again without the intervention of any other spore stages. No trace of pycnia was found. In 1905 Fischer (14) reported the culture of the short cycle species of Uromyces which occurs in Europe as well as in America, U. Solidaginis. He sowed teliospores upon Solidago Virgaurea alpestris, and in about 13 days noted the infection upon the leaves; telia were produced, but in no case were pycnia to be observed. While North American material of this species has not been cultured, it is supposed that similar conditions obtain here. Schneider (24) cultured U. Scillarum (Grev.) Wint., a short cycle form, and reported specialization as to hosts. The teliospores were found to be capable of germination, either at once or after a period of rest. No cultures of endemic North American short cycle Uromyces seem to have been reported. CARLETON (8), ARTHUR (3), and others, however, have reported cultures of some species of lepto-Puccinia. WILLE (27) recently found a sharp specialization of the lepto-form Puccinia Arenariae upon the different host genera attacked.

The evidence obtained from cultures indicates that similar conditions exist in the short cycle forms, both of *Uromyces* and *Puccinia*.

A greater specialization and fixity may exist with short cycle forms than with forms with long life cycles; of course fewer spore forms upon which variability may be manifested are present.

Pycnia may be produced, under certain conditions, in some of these short cycle species of *Uromyces* not yet known to produce pycnia. It is to be noted, however, that species in which the teliospores germinate at maturity, that is, lepto-forms, seldom produce pycnia. Teliospores cannot function directly as repeating spores, but in lepto-forms a comparatively rapid repetition is secured through the intervention of the basidiospores, which are produced immediately upon maturity of the teliospores.

Cytological work upon the short cycle rusts indicates that similar conditions obtain with the short cycle species, both of Uromyces and Puccinia. The work of SAPPIN-TROUFFY (23) upon the histology of the rusts included a study of the short cycle forms Uromyces Ficariae (Schum.) Lev. and Puccinia malvacearum Mont. His observations were corroborated and extended with the two rusts, among others, by Blackman and Fraser (7). They found that the general vegetative mycelium of Uromyces Ficariae consists of uninucleate cells, some of the later vegetative, together with the sori-forming, mycelium being binucleate. They found similar conditions for Puccinia malvacearum, the binucleate condition evidently arising at several different points for each sorus, shortly before the sorus is formed. Blackman and Fraser also observed that the short cycle forms Puccinia Adoxae Hedw.f. and Uromyces Scillarum (Grev.) Wint. had a binucleate rather than a uninucleate general vegetative mycelium, and suggested that it is "probable that in these two forms the conjugate condition is produced soon after infection by nuclear migration, or by cell fusion, between vegetative cells." Olive (20) discussed and figured sexual fusions near the base of the telium in a short cycle form, Puccinia transformans Ellis and Ev. Dealing with North American rusts, OLIVE (19) also reported that differing conditions as to the sporophytic and gametophytic generations occurred with certain short cycle Puccinia forms; while Uromyces Rudbeckiae Arth. and Holw. showed the anomalous extreme of possessing uninucleate cells through all the mycelium and sorus, even including the teliospores.

This phenomenon he was not able to explain fully. Other papers to be noted are those by Werth and Ludwigs (26), Hoffman (16), and Moreau (18). A considerable summary of recent cytological work is presented by Ramsbottom (22).

From this work it appears that the duration of the binucleate stage varies in different species of short cycle rusts, being brief, extended, or intermediate. Fusions between cells initiate this binucleate condition. Some life history problems, including the

TABLE I

HOST RELATIONSHIPS OF SHORT CYCLE Uromyces

Host -	Species of Uromyces	Distribution	Mycelium	Common condition of germination	Pycnia
Liliaceae Erythronium	U. heterodermus	Rockies	Local or rather diffuse	Micro	Present
Cassiaceae Bauhinia Bauhinia	U. bauhiniicola U. jamaicensis	S.W. Mexico Mexico; West Indies	Rather diffuse Local	Micro Micro	Present Present
Fabaceae Psoralea	U. abbreviatus	Pacific Coast	Local, becoming rather diffuse	Micro	Present
Euphorbiaceae Chamaesyce Tithymalus	U. Tranzschelii	Western N.A.	Diffuse	Micro	Present
Primulaceae Primula	U. nevadensis	Western N.A.	Local or rather diffuse	Micro	Not knows
Myrsinaceae Myrsines	U. Myrsines	Costa Rica; S.A.	Local	Micro	Not known
Carduaceae Solidago Anaphalis Rudbeckia Bidens	U. Solidaginis U. amoenus U. Rudbeckiae U. Bidentis	W.N.A.; Europe Western N.A. Central N.A. Porto Rico; S.A.	Local Local Local Local	Micro Micro Lepto Lepto	Not known Not known Not known Not known

relative importance and relation of cell and nuclear fusions, some relations in the formation of pycnia in short cycle forms, the presence of perennial mycelium, etc., appear not to have been fully determined.

Hosts

The range of hosts attacked by these North American short cycle species of *Uromyces* embraces both the monocotyledons and dicotyledons. The situation is shown in table I.

Foreign species of short cycle *Uromyces* fill in several families not represented here. The wide range of hosts attacked indicates that these rusts do not form a restricted group; one might expect

to find affiliations with other forms of rusts upon the same or similar hosts through the various families, and such is the case. Under the species *U. heterodermus* a considerable comparison with rusts from related hosts is made, suggesting that certain groups of hosts appear to harbor rusts characterized by various definite morphological characters.

The geographical distribution of North American short cycle species of *Uromyces* would indicate further that the mountainous and more tropical regions furnish the most favorable location for these forms. Only *U. Rudbeckiae* has a comparatively wide range, a range including the plains area.

Whether or not it is more than a coincidence that the absence of pycnia and the occurrence of lepto-germination are found on hosts higher in the evolutionary scale, the writer is not prepared to say.

Taxonomic

With the progress of critical studies of North American rusts, other short cycle forms will undoubtedly be separated out, and further evidence secured as to the fixity and definiteness of the life cycle in certain of these rusts. *Uromyces heterodermus*, for example, was long placed with *U. Erythronii*, a correlated form. It was found also that *U. Bidentis* was a short cycle form which resembled *U. bidenticola* (P. Henn.) Arth. so far as characters of teliospores are concerned. It is no doubt true that other short cycle forms have been collected and placed with correlated long cycle forms, although cultures are needed to determine the life cycle in certain cases.

The II species of *Uromyces* considered have several points of similarity, one of which is the fact that all possess teliospores with apices more or less thickened. In none of the species were paraphyses, stromata, isolated peridial cells, or other accompanying structures found in the telia.

KEY

Teliospores verrucose.

Teliospores reticulate.		
Spores 14-21 by 18-26 \(\mu \cdots \	2.	U. bauhiniicola
Spores 12-17 by $16-23 \mu \dots \dots$		U. jamaicensis
Teliospores smooth.		
Wall thin, 1-1.5 μ .		
Spores narrow, 11-17 \mu wide.		
Spores 27-39 μ long	7.	U. Myrsines
Spores 19-32 μ long	10.	U. Rudbeckiae
Spores broad, 15-28 μ wide		Contract to the second
Wall thick, τ. 5-3 μ.		
Apex thickened 6-12 μ	8.	U. Solidaginis
Apex thickened $3-7 \mu$.		
Spores 27-40 μ long	4.	U. abbreviatus
Spores 19–30 μ long	9.	U. amoenus

1. Uromyces heterodermus Sydow, Ann. Myc. 4:29. 1906.

O. Pycnia amphigenous, not uncommon, gregarious in loose groups with the telia, 0.5–1.5 mm. across, inconspicuous, subepidermal, dark golden-brown, flattened globoid, 100–185 μ in diameter by 65–130 μ in height; ostiolar filaments few, loose, up to 65 μ long.

III. Telia amphigenous, numerous, scattered or in small groups, sometimes upon inconspicuous spots, roundish or oval, o.3–2 mm. across, rather early naked, pulverulent, dark cinnamon-brown, surrounding epidermis noticeable; teliospores ellipsoid or broadly ellipsoid, $19-26\times26-43~\mu$, rounded above, rounded or slightly narrowed below; wall dark golden-brown, 1.5 μ thick, thickened at the apex with a distinct hyaline papilla, 3–6 μ , coarsely verrucose above, with the markings often in longitudinal ridges, smoother below; pedicel hyaline, fragile, short.

On LILIACEAE: Erythronium grandislorum Pursh, Colorado, Montana, Utah, Washington, British Columbia; E. montanum S. Wats., Washington; E. obtusatum Goodding, Wyoming; E. parvislorum (Wats.) Goodding (E. grandislorum parvislorum S. Wats.), Colorado, Montana, Oregon, Utah, Washington, Wyoming.

Type locality: Wasatch Mountains, Utah, on Erythronium parviflorum. Distribution: Rocky Mountain region from Colorado and Utah northward, and to the coast in Oregon.

EXSICCATI: Barth., Fungi Columb. 4694; Barth., N.Am. Ured. 789, 1592, 1692; Garrett, Fungi Utah. 118; Ellis and Ev., Fungi Columb. 750.

LITERATURE: Sydow, Monog. Ured. 2:270. 1910; SACCARDO, Syll. Fung. 21:579. 1912.

This rust, previous to Sydow's description in 1906, passed as U. Erythronii (DC.) Pass., a related European species possessing aecia. Thus Ellis and Everhart's Fungi Columbiani 750 was issued as U. Erythronii. The host of this collection is undoubtedly Erythronium parviflorum; earlier collections of this host were frequently considered, as in this case, to be E. grandiflorum.

This rust occurs upon the species of Erythronium found in the western part of North America. According to Engler (Engler and Prantl, Nat. Pflanz. 25:60. 1888) species of Erythronium occur particularly in North America. He places the following genera together to constitute the section Liloideae-Tulipeae: Lilium, Fritillaria, Erythronium, Tulipa, Lloydia, and Calochortus. Several rusts occur upon these genera of hosts. For the sake of comparison, all such rusts are tabulated. To avoid a personal factor, the data are largely from the Sydows' Monograph, and any supplementary data obtained are added in brackets. Parentheses indicate a rather free translation. Some data are taken from a paper by Rees (Amer. Jour. Bot. 4:368–373. 1917), who also presents drawings which support the contention that the rusts on these hosts possess rather unusual morphological similarities.

Table II shows many points of similarity in these rusts. It is to be noted that practically all possess amphigenous, rounded or minute, pulverulent sori, with spores broadly ellipsoid, rather similar as to size, with the wall usually moderately thick, apex somewhat thickened with a papilla, pedicel hyaline and short; and especially, all possess, in a striking manner, surface markings usually striate or verrucose and arranged in rows. This unanimity in morphological characters would indicate that a closely and definitely related group of rusts occurs upon these related hosts. Correlations, more or less perfect, obtain throughout this group of rusts upon the Liloideae-Tulipeae, and are found to extend further through the Liliaceae. Figs. 1–6 illustrate, for comparison, the teliospores of three of these rusts.

2. Uromyces Bauhiniicola Arth. Bot. Gaz. 39:389. 1905.— Telospora Bauhiniicola Arth., Result. Sci. Congr. Bot. Vienne 346. 1906.

TABLE

LILOIDEAE-TULIPEAE OF RUSTS

Character of telia	Pulverulent		Pedicel	Hyaline, short Hyaline, deciduous Hyaline, deciduous Hyaline, short	
Shape of telia	mphigenous		Sculpturing	Coarsely verrucose in rows Rugose in rows Rugose or verrucose in rows Verrucose in rows Rugose in rows Rugose in rows Reticulate-striolate Verrucose in rows Verrucose in rows Rugose in ridges Verrucose Hyal Hyal Hyal Hyal	
Leaf surface bearing telia					
Geographical l	Am A		Apex character	Hyaline papilla Hyaline papilla Hyaline papilla Hyaline papilla Hyaline apiculus Hyaline apiculus Hyaline papilla Hyaline papilla Hyaline papilla Hyaline papilla Apiculus Apiculus (Aculeate)	
Geog	Europe (N.A.?) Europe Japan Japan Japan Japan Japan Japan N.A. N.A. Europe Europe Europe Europe Europe		Apex in	10 5] [to 5] [to 5] [to 5] [to 5] [5-7] [5-7] [3-5] [3-5]	
Life cycle			Wall in	About 3 2-3.5 1.5-2 3-6 3-6 1.5-2 1.5-2 [2-2.5] [1.5-2.5] [1.5-2.5] [1.5-2.5]	
Source of data	This paper Rees Sydow Hill Sydow Sydow Hill Sydow Sydow Sydow Hill Sydow		Size of teliospores	19-26 X 26-43 23-27 X 31-35 22-30 X 28-44 16-25 X 22-42 26-32 X 26-38 14-23 X 24-35 26-32 X 26-38 26-32 X 26-38 26-32 X 26-38 26-32 X 26-40 20-28 X 28-46 20-28 X 28-46 20-28 X 24-42 34-40 X 54-66 21-32 X 30-44	
Host genus	Erythronium (Fritillaria?) Lilium Fritillaria Fritilla		General shape of teliospores	Broad, ellipsoid Broad, ellipsoid Broad, ellipsoid (Broad, ellipsoid Subglobose Ellipsoid Broad, ellipsoid Broad, ellipsoid Ovate Broad, ellipsoid	
Rust	Uromyces heterodermus Sydow. (Uromyces aecediiformis (Strauss) Rees. (Uromyces Lilii (Link) Fuckel. Uromyces Erythronii (DC.) Pass. Uromyces Miurae Sydow. Uromyces Fritillaria (Schlechtd.) Thüm. Uromyces Tulipae Dietel. Uromyces Japonicus Sydow. (Uromyces Japonicus Sydow. (Uromyces Holwayi Lagerh. (Uromyces Holwayi Lagerh. (Uromyces Holwayi Lagerh. (Uromyces Holwayi Lagerh. (Uromyces Holwayi Sydow. (Uromyces Holwayi Lagerh. (Ur		Rust	Uromyces heterodermus Sydow. (Uromyces aecidiiformus (Strauss) Rees. (Uromyces Lilii (Link) Fuckel. Uromyces Erythronii (DC.) Pass. Uromyces Miurae Sydow. Uromyces Miurae Sydow. Uromyces Fritillaria (Schlechtd.) Thüm. Uromyces Tulipae Dietel. Uromyces Holwayi Lagerh. (Uromyces Holwayi Lagerh. (Uromyces Holwayi Lagerh. (Nigredo Lilii (Clint.) Arth. Puccinia Calochorti Peck. Puccinia Prostii Mong. Puccinia Tulipae Schroet.	

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O. Pycnia epiphyllous, few, gregarious in small groups, usually opposite the telia, punctiform, subepidermal, brownish, flattened globose, $60-130~\mu$ in diameter by $30-65~\mu$ in height; ostiolar filaments compact, short.

III. Telia at first hypophyllous, becoming also somewhat epiphyllous, numerous, scattered or in small groups, roundish, small, 0.2–1 mm. across, early naked, pulverulent, chocolate-brown, surrounding epidermis inconspicuous; teliospores globoid or broadly ellipsoid, 14–21 by 18–26 μ , rounded at the ends; wall cinnamon or chestnut brown, thick, 2.5–4 μ , apex thicker, 4–7 μ , with a paler, broad umbo, finely reticulated; pedicel pale or colorless, often roughened below, rather fragile but sometimes two or three times as long as the spore.

On Cassiaceae: Bauhinia Pringlei S. Wats., Jalisco; Bauhinia sp., Guerrero.

Type locality: Guadalajara, Mexico, on Bauhinia Pringlei.

DISTRIBUTION: Known only from Southwest Central Mexico.

ILLUSTRATION: Ark. Bot. Stockh. 4: pl. 1. fig. 9.

Exsiccati: Barth., N.Am. Ured. 286.

LITERATURE: VESTERGREN, Ark. Bot. Stockh. 4:28-29. 1905; Sydow, Monog. Ured. 2:80, 81. 1909; SACCARDO, Syll. Fung. 21:550-551. 1912.

- 3. Uromyces Jamaicensis Vesterg. Ark. Bot. Stockh. 4:33. 1905.
- O. Pycnia chiefly epiphyllous, gregarious in small groups with the telia, subepidermal, brownish, flattened, 60–100 μ in diameter by 45–70 μ in height; ostiolar filaments compact, hardly extending beyond the ostioles.
- III. Telia amphigenous, numerous, gregarious in small groups or occurring singly, sometimes on small yellowish spots, roundish, small, o. 1–1 mm. across, early naked, pulverulent, chestnut-brown, surrounding epidermis noticeable; teliospores globoid, broadly ellipsoid or obovoid, $12-17\times16-23~\mu$, rounded or slightly narrowed at the ends; wall cinnamon-brown, $1.5-2~\mu$ (sometimes up to $3.5~\mu$) thick, thicker at the apex, up to $5~\mu$, with a lighter crater or capshaped crown, closely and finely reticulate, appearing verrucose under the lower powers of the microscope; pedicel pale, fragile, $4-15~\mu$ long.

On Cassiaceae: Bauhinia divaricata L., Cuba, Guanajuoto; B. Pauletia Pers., Porto Rico; B. porrecta Sw., Jamaica.

Type locality: Constant Spring, Jamaica, on Bauhinia sp.

DISTRIBUTION: Mexico and the West Indies.

Illustration: Ark. Bot. Stockh. 4: pl. 2. fig. 14.

LITERATURE: Sydow, Monog. Ured. 2:84. 1909; SACCARDO, Syll. Fung. 21:552-553. 1912.

This species may perhaps be distinguished from the preceding by the somewhat reduced length and breadth of the teliospores, the wall thickness often being less also. The differences described by Vestergren (loc. cit.) have not been found to hold entirely throughout the collections at the Arthur herbarium. Some differences, however, are still to be found between the two species of rust, and they are maintained as separate species, at least pending further collections.

Vestergren's supposition that *Uromyces jamaicensis* is a micro-*Uromyces* has been corroborated by the discovery of pycnia associated with telia upon a Cuban specimen of *Bauhinia divaricata*. The specimen upon *B. porrecta* collected by Thaxter has not been seen, but Vestergren's type collection has been examined.

Vestergren separated 17 species of *Uromyces* upon the host *Bauhinia*, for none of which aecia are known. Evident similarities are shown between the species as he described and figured them. *Uromyces* only are known to occur upon *Bauhinia*. Many species of *Bauhinia* occur in the tropics; related genera, as shown by Engler and Prantl's classification, are chiefly genera upon which rusts have not yet been found. The reticulate nature of the sculpturing upon the surface of the teliospores of these two species is minute, but evident under higher microscopic power. Figs. 7–10 illustrate the two species.

- 4. Uromyces abbreviatus Arth. Bull. Torr. Bot. Club 42:587. 1915.
- O. Pycnia hypophyllous, scattered among the telia, inconspicuous, subepidermal, deep seated, dark honey-yellow, globose or flattened globose, 115–200 μ in diameter by 95–140 μ in height; ostiolar filaments dense, often falling away, up to 60 μ in length.
- III. Telia hypophyllous, rarely also epiphyllous, densely clustered, becoming scattered over considerable areas, roundish,

0.2–0.7 mm. across, early naked, pulverulent, chocolate-brown, surrounding epidermis at first evident, later often hidden by the loose spores; teliospores ellipsoid or irregularly obovoid, $21-26\times27-40~\mu$ (sometimes variable in size, and larger), rounded above, rounded or narrowed below; wall chestnut-brown, $1.5-3~\mu$ thick, apex $3-5~\mu$ thick, often with a slight umbo over the pore, smooth; pedicel colorless, delicate, fugacious, half as long as the spore or less.

On Fabaceae: Psoralea physodes Dougl., California, Washington, British Columbia; P. Purshii Vail, Nevada.

Type locality: Winnemucca, Nevada, on Psoralea Purshii.

DISTRIBUTION: Pacific Coast region, west of the mountains, from British Columbia to California.

Exsiccati: Barth., N.Am. Ured. 1582; D. Griff., W.Am. Fungi 390; Barth., Fungi Columb. 4884.

The type of this species is GRIFFITH'S West American Fungiago, which was issued as Uromyces Psoraleae Peck. U. Psoraleae possesses aecia, however. U. abbreviatus, while without aecia, and possessing pycnia with the telia, resembles U. Psoraleae in the telial stage, as indicated by ARTHUR in the notes with the original description. While U. Psoraleae extends to the Pacific Coast, it is more common in the Rocky Mountain region, and extends over the plains to the east of the mountains. U. abbreviatus, so far as known, is limited to the region west of the Rockies.

There is an unconnected Aecidium (Aecidium onobrychidis Burrill, Bull. Ill. State Lab. Nat. Hist. 2:225. 1885) upon Psoralea Onobrychis, represented as far as known by the one collection by Seymour in Illinois, and distributed by Ellis and Everhart as North American Fungi 1826. No other species of rust are reported for the genus Psoralea, and these species are only known in North America. Related hosts, as given by Engler and Prantl, except for the genus Indigofera in an adjoining section, are scarcely known to be attacked by rusts; no closely related rusts are evident upon related hosts.

While the type collection is from an altitude of about 5000 ft., other collections in the Arthur herbarium are from nearer the coast, at much less altitude, extending almost down to sea-level.

- 5. Uromyces Tranzschelii Sydow; Tranzschel, Ann. Myc. 8:20. 1910.
- O. Pycnia hypophyllous, scattered among the telia, or in groups, noticeable, subepidermal, dark yellow, globoid or flask-shaped, 100–145 μ in diameter by 75–130 μ in height; ostiolar filaments dense, agglutinated into a truncate column, 50–80 μ in height, 50–70 μ in diameter at the ostiole.

III. Telia hypophyllous, occasionally sparingly epiphyllous, numerous, evenly scattered over large areas, or sometimes in groups around the pycnia, roundish, 0.2–0.6 mm. across, early naked by a central pore, pulverulent, chestnut-brown, surrounding epidermis crateriform, conspicuous; teliospores globoid or ellipsoid, $15^{-22} \times 19^{-30} \mu$, rounded at the ends, wall cinnamon-brown, $1.5^{-2.5} \mu$ thick, apex 3–5 μ thick with a low, sub-hyaline apiculus, minutely verrucose, the markings often in irregular longitudinal lines; pedicel colorless, deciduous.

ON EUPHORBIACEAE: Chamaesyce serpens (H.B.K.) Small (Euphorbia serpens H.B.K.), California; Tithymalus montanus (Engelm.) Small (Euphorbia montana Engelm.), Colorado, New Mexico, Utah, Wyoming; T. robustus (Engelm.) Small (Euphorbia montana robusta Engelm.), Colorado, Utah, Wyoming; Tithymalus sp. (Euphorbia Palmeri Engelm.), Lower California.

Type locality: Colorado, on Euphorbia montana.

DISTRIBUTION: From Wyoming to New Mexico, California, and Lower California.

Exsiccati: Barth., N.Am. Ured. 499; Ellis and Ev., Fungi Columb. 1069; Ellis and Ev., N.Am. Fungi 2230; Garrett, Fungi Utah. 97.

LITERATURE: TRANZSCHEL, Ann. Myc. 8:1-35. 1910; SYDOW, Monog. Ured. 2:171-172. 1910; SACCARDO, Syll. Fung. 21:560-561. 1912; DIETEL, Hedw. 28:185-187. 1889; Arthur, Bull. Torr. Bot. Club 45:152. 1918.

This rust passed as *Uromyces scutellatus* (Schrank.) Lev., a European species, until Sydow's description in 1910. Tranzschell pointed out that *U. Tranzschelii* is similar to *U. monspessulanus* Tranz.; indeed, other similarities to various Euphorbiaceous rusts are evident. In his study of the autoecious rusts upon *Euphorbia*, Tranzschel stated that most European autoecious species with telia from diffused mycelium had passed as two species, *Uromyces scutellatus* or *U. excavatus*; he divided such forms into some 12 species, and found a total of 27 autoecious species of *Uromyces*

upon hosts belonging to the various sections of the genus *Euphorbia*. That these species are related is evidenced by the fact that many had passed under one name; furthermore, many similarities are to be noted from Tranzscheli's descriptions. For example, all but one species are listed as having verrucose or striolate teliospore walls. A table showing characters in a manner similar to those tabulated under *U. heterodermus* would be illuminating as indicating relationships between *U. Tranzschelii* and other species of rust upon related hosts. The writer considered it sufficient, however, to call attention to Tranzscheli's work as indicating relationships. Certain heteroecious species with aecia upon *Euphorbia* likewise show resemblances to *U. Tranzschelii*.

Both Ellis and Everhart's Fungi Columbiani 1069 and North American Fungi 2230 were issued as *U. scutellatus*, while Garrett's Fungi Utahensis 97 was issued as *U. andinus* P. Magn., a related South American rust.

The range of *U. Tranzschelii* begins at about the western limit of the range of the related species *U. proeminens* (DC.) Pass., and continues westward to the Pacific Coast. Range conditions comparable with those of *U. abbreviatus* are thus shown, and neither of these short cycle forms necessarily occurs at high altitudes.

Tranzscheli. (loc. cit., p. 20) considered the rust upon Euphorbia Palmeri to be different, apparently another species. The specimen studied by the writer is not considered different from other specimens of U. Tranzschelii.

Dietel (loc. cit.) commented upon Ellis and Everhart's North American Fungi 2230, especially concerning the relationship of an Aecidium upon the same host distributed as no. 2215 of the same exsiccati. It is true that Aecidium Tithymali Arth. occurs upon the same hosts, sometimes upon the same leaves, as Uromyces Tranzschelii. The situation in regard to this Aecidium Tithymali is uncertain. Germination tests show that it is a true Aecidium and not an Endophyllum. Its alternate host, however, has not been found. Arthur (loc. cit.) has discussed this Aecidium and its possible relation to U. Tranzschelii.

6. Uromyces nevadensis Hark. Bull. Calif. Acad. Sci. 1:36. 1884.—Caeomurus nevadensis Kuntze, Rev. Gen. 33:450. 1898.

O. Pycnia unknown.

III. Telia amphigenous, circinating in groups 2-5 mm. across, or somewhat scattered, round or oval, 0.2-1.0 mm. across, early naked, pulvinate, becoming somewhat pulverulent, chestnut-brown, ruptured epidermis conspicuous; teliospores oblong, oblong-obovoid, or ellipsoid, $19-27\times29-47$ μ , rounded at the apex, rounded or narrowed toward the base; wall cinnamon-brown, lighter or colorless at the apex, moderately thick, 1.5-2.5 μ , thickened at the apex, 5-7 μ , moderately and rather finely verrucose; pedicel colorless, fragile.

ON PRIMULACEAE: Primula suffrutescens Gray, Nevada.

Type locality: Lake Tahoe, Nevada, on P. suffrutescens.

DISTRIBUTION: Known only from the type locality.

Literature: Magnus, Ber. Deutsch. Bot. Gesells. 18:451-459. 1900.

Illustration: Magnus, loc. cit. pl. 16. figs. 16-19.

The writer is considerably indebted to the members of the botanical staff at the Purdue Station for the preceding. ARTHUR in a letter states that "a careful study of this species seems to leave little doubt that it is a distinctly American species and a short cycle one. This was the conclusion reached by Magnus in 1900." The one collection known was made by Harkness, and a specimen has been studied by the writer.

7. Uromyces Myrsines Diet. Hedwigia 36:26. 1897.

O. Pycnia unknown.

III. Telia hypophyllous, crowded upon reddish or brownish spots 2–10 mm. in diameter, margin of spots usually elevated, roundish, 0.1–0.2 mm. in diameter, often confluent, early naked, pulvinate, light chocolate-brown, ruptured epidermis inconspicuous; teliospores oblong or oblong-ellipsoid, $13-16\times27-39~\mu$, rounded or acute above, narrow below; wall pale golden-brown, rather thin, $1-1.5~\mu$, thickened at the apex, $3-8~\mu$, smooth; pedicel colorless, short.

On Myrsinaceae: Ardisia compressa H.B.K., Costa Rica.

Type locality: Rio de Janeiro, Brazil, on Myrsine sp.

DISTRIBUTION: Costa Rica; also in South America.

LITERATURE: ARTHUR, Mycologia 10:124, 1918; Sydow, Monog. Ured. 2:46. 1909.

This rust was known only from South America before its discovery by Holway in one locality in Costa Rica. South American specimens have been distributed by E. Ule, Herbarium Brasiliense no. 2136. Arthur suggests that *U. marginatus* Bomm. and Rouss may be a synonym. Sydow gives *U. Rhapaneae* Henn. and *U. Usterianus* Diet. as synonyms. While Sydow was probably right, it has been impossible to examine specimens of these two collections.

8. UROMYCES SOLIDAGINIS (Sommerf.) Niessl, Verh. Natur. Ver. Brunn 10:163. 1872.—Caeoma Solidaginis Sommerf. Suppl. Fl. Lapp. 234. 1826; Caeomurus Solidaginia Kuntze, Rev. Gen. 33:450. 1898; Telospora Solidaginia Arth., Result. Sci. Congr. Bot. Vienne 346. 1906.

O. Pycnia not found; probably wanting.

III. Telia hypophyllous, sometimes also petiolicolous or caulicolous, crowded and often confluent in orbicular groups upon the leaves, or in elongated groups upon the petioles or stems, 2–10 mm. across, upon yellowish spots, roundish, small, 0.3–0.7 mm. across, early naked, compact, pulvinate, chocolate-brown, surrounding epidermis noticeable; teliospores obovate or ellipsoid, $17-25 \times 24-33 \mu$, narrowed or rounded at the ends; wall chestnut-brown, $1.5-3 \mu$ thick, much thicker at the apex, $6-12 \mu$, smooth; pedicel nearly colorless, about as long as the spore.

On Carduaceae: Solidago polyphylla Rydb., Colorado; S. serotina Ait., Montana, Washington, Wyoming.

Type locality: Nordland, Sweden, on Solidago virgaurea.

DISTRIBUTION: Colorado to Montana and Washington, also in Europe and Asia.

ILLUSTRATIONS: Archiv. Naturw. Land. Bohmen 13: fig. 12; Beitr. Krypt. Schweiz 22: fig. 44.

EXSICCATI: D. Griff., W.Am. Fungi 361; Ellis and Ev., N.Am. Fungi 2883.

LITERATURE: COOKE, Grev. 5:152. 1877; WINTER, in Rab. Krypt.

Fl. 1¹:141. 1881; SACCARDO, Syll. Fung. 7:566. 1888; FISCHER, Beitr. Krypt.

Schweiz 2²:59, 543. 1904; FISCHER, Ber. Schw. Bot. Gesells. 15:(1-2). 1905;

HARIOT, Les Ured. 216. 1908; Sydow, Monog. Ured. 2:10. 1909.

This is the one species of *Uromyces* included in this paper which is not endemic to the Americas. Fischer (1905) reported cultures of this rust. He also (1898) pointed out the correlation between this species and *U. Junci* (Desmaz.) Tulasne, which bears aecia

upon hosts related to Solidago. The range of both U. Solidaginis and U. Junci in North America is similar, both occurring in the western part.

Uromyces Junci-effusi Sydow resembles U. Solidaginis in the telial stage; the aecial connection is not known for this form. Curiously not Puccinia Solidaginis Peck, but P. Asteris Duby (both are short-cycled) shows a correlation with Uromyces Solidaginis. Of the short cycle species of Puccinia upon Solidago in America, one, P. Virgauriae (DC.) Lib., is more eastern, possesses stromata, and has thin-walled teliospores. P. Solidaginis, although a western form, has very large teliospores. P. Asteris, however, is very similar to Uromyces Solidaginis in gross and microscopic characters, except in the possession of 2-celled teliospores. Puccinia Asteris is a more common rust, and while rare west of the Rockies, is found over most of North America. Figs. 19-22 illustrate U. Solidaginis from America and Europe and P. Asteris.

COOKE (loc. cit.) reported Uromyces Solidaginis from Maine. Collections from Eastern North America are not at hand; further doubt may be attached to Cooke's reported collection from the fact that he states that the spores are reticulated. Griffith's West American Fungi 361, although issued as Puccinia Solidaginis, is in reality Uromyces Solidaginis.

- 9. Uromyces amoenus Sydow, Ann. Myc. 4:28. 1906.
- O. Pycnia unknown.

III. Telia hypophyllous, densely grouped and often confluent on circular purplish spots, 2–8 mm. across, the margin of the spots yellow, roundish, small, 0.2–0.7 mm. across, early naked, compact pulvinate, dark chestnut-brown, covered by the tomentose pubescence of the host, ruptured epidermis inconspicuous; teliospores globoid, obovoid, or ellipsoid, $16-23\times20-30~\mu$, usually rounded above and narrowed below; wall dark golden-brown or cinnamonbrown, moderately thick, $1.5-2.5~\mu$, apex thicker, $4-7~\mu$, smooth; pedicel pale yellowish, up to the length of the spore.

On Carduaceae: Anaphalis margaritacea occidentalis Greene, Oregon; A. subalpina (A. Gray) Rydb. (A. margaritacea subalpina A. Gray), Idaho, Oregon, Washington, Wyoming, British Columbia.

Type locality: Washington, on "Gnaphalium (Anaphalis) margaritacea." Distribution: Wyoming to British Columbia and Oregon.

EXSICCATI: Ellis and Ev., Fungi Columbiani 1795; Barth., N.Am. Ured. 1385, 1584.

LITERATURE: SYDOW, Monog. Ured. 2:4. 1909; SACCARDO, Syll. Fung. 21:570. 1912.

Several collections of this rust are in the Arthur herbarium. Although the hosts of some collections are labeled *Anaphalis margaritacea*, it would appear that the name *A. subalpina* should be used for almost all collections in hand (compare Coulter and Nelson, New Manual of the Botany of the Central Rocky Mountains, p. 537).

Ellis and Everhart's Fungi Columbiani 1795 was issued as Uromyces Gnaphalii Ellis and Ev., but is U. amoenus. U. Gnaphalii has been found to be a synonym of U. intricatus Cooke.

10. UROMYCES RUDBECKIAE Arth. and Holw. Bull. Iowa Agric. Coll. 1884. 154. 1885.—Caeomurus Rudbeckiae Kuntze, Rev. Gen. 3³:450. 1898; Telospora Rudbeckiae Arth., Result. Sci. Congr. Bot. Vienne 346. 1906.

O. Pycnia unknown.

III. Telia hypophyllous, occasionally also epiphyllous, densely gregarious upon brownish spots, paler below, 1–10 mm. across, rather circinate, small, 0.2–0.8 mm. in diameter, early naked, compact, pulvinate, cinnamon-brown, soon cinereous from germination, surrounding epidermis not noticeable; teliospores ellipsoid, obovoid, or pyriform, $11-17\times19-32~\mu$, rounded, acute, or obtuse at the apex, narrowed below; wall yellowish or very pale chestnut-brown, thin, $1~\mu$, apex thicker, $5-8~\mu$, smooth; pedicel hyaline, twice as long as the spore or less.

On Carduaceae: Rudbeckia laciniata L. (R. ampla A. Nels.), Colorado, Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, Montana, Nebraska, New Mexico, North Dakota, Pennsylvania, Wisconsin, Wyoming, Ontario; Rudbeckia sp., Texas.

Type locality: Decorah, Iowa, on Rudbeckia laciniata.

DISTRIBUTION: Ontario and Pennsylvania to Montana and Texas.

ILLUSTRATION: Arth. and Holw. Ured. Exs. Ic. 1: pl. 1. fig. 1.

Exsiccati: Arth. and Holway, Ured. Exs. Ic. 1: Barth., Fungi Columb. 4394; Barth., N.Am. Ured. 299, 1099, 1397; Brenckle, Fungi Dak. 274; Ellis and Ev., Fungi Columb. 2097; Ellis, N.Am. Fungi 1439; Rab.-Wint., Fungi Eur. 3412; Sydow, Ured. 1305, 1962.

LITERATURE: BURRILL, Bull. Ill. State Lab. Nat. Hist. 2:163. 1885; SACCARDO, Syll. Fung. 7:581. 1888; ARTHUR and Holway, Bull. Lab. Nat. Hist. State Univ. Iowa 3:44. 1895; Sydow, Monog. Ured. 2:7-8. 1909.

Uromyces Rudbeckiae has been collected more frequently than any North American species of the group. Its range embodies the greater part of the plains area, and extends to the Rocky Mountains.

DIETEL (Ann. Myc. 8:305. 1910) considered *Uromyces Komerovii* Bubak on *Solidago Virgaurea* identical with *U. Rudbeckiae*. No specimens of the former have been seen, although a collection on *Solidago Virgaurea* in the herbarium has not been found to differ from *U. Solidaginis*.

The only other rust found upon Rudbeckia is Aecidium Compositarum Auct., recently found to belong with U. perigynius Halsted (Mycol. 9:307), a connection suspected from the fact that the telial stage of U. Rudbeckiae is similar to the telial stage of U. perigynius. A type of correlation which has frequently been of service in indicating alternate stages of heteroecious rusts is thus evidenced. The cytological work upon this species is noted earlier in this paper.

11. UROMYCES BIDENTIS Lagerh. Bull. Soc. Myc. Fr. 11:213, 1895.—Caeomurus Bidentis Kuntze, Rev. Gen. 33:449. 1898; Uromyces densus Arth. Mycologia 7:196. 1915.

O. Pycnia unknown.

III. Telia hypophyllous, numerous, in small circinating groups on roundish, discolored spots, 1–4 mm. across, sometimes confluent, roundish or oval, 0.1–1 mm. across, the central sorus larger, surrounded by smaller ones, early naked, compact, pulvinate, dull cinnamon-brown, becoming waxy-cinereous from germination, surrounding epidermis inconspicuous; teliospores obovoid or oblong, $15-28\times30-45~\mu$, rounded or narrowed above, narrowed below; wall pale golden or cinnamon-brown, thin, $1~\mu$, thicker above, $4-9~\mu$, smooth; pedicel hyaline, once or twice the length of the spore or less.

On Carduaceae: Bidens leucantha (L) Willd., Porto Rico; B. pilosa L., Porto Rico; Bidens sp., Costa Rica.

Type locality: Ecuador, South America, on Bidens andicola.

DISTRIBUTION: Porto Rico and Central America; also in South America.

The Sydows (Monog. Ured. 1:3. 1909) misapplied Lager-Heim's name to the species with uredinia, now called *Uromyces bidenticola* (P. Henn.) Arth. The situation in regard to these two rusts is discussed by Arthur (Mycologia 9:71. 1917), and he also (Mycologia 10:127. 1918) suggests that it is possible that a fixity of life cycle may not occur in these *Bidens* rusts. *U. Bidentis* is correlated with *U. Bidenticola*, differing only in the life cycle and in the characters of the telia, which are coalescent and thickened into cushions in *U. Bidentis*. Specimens are at hand also from South America; Lagerheim's collection from the type locality has been examined.

Puccinia Bidentis Diet. and Holw., Bot. GAZ. 24:32. 1897, collected by Holway in Mexico, apparently is not a correlated species.

EXCLUDED SPECIES

UROMYCES HYALINUS Peck, Bot. Gaz. 3:34. 1878.—U. Sophorae Peck, Bull. Torr. Bot. Club 12:35. 1885; Caeomurus hyalinus Kuntze, Rev. Gen. 3³:450. 1898; Telospora hyalina Arth., Result. Sci. Congr. Bot. Vienne 346. 1906.

LITERATURE: SACCARDO, Syll. Fung. 7:581. 582. 1888; HARIOT, Revue Mycol. 14:21. 1892; Sydow, Monog. Ured. 2:128. 1909.

This rust, first described upon Sophora sericea from Colorado, and made the type of the genus Telospora, has been found to possess uredinia. Olive, in his paper on intermingling of perennial sporophytic and gametophytic generations, etc. (Ann. Myc. 11:309. 1913), mentions that Arthur has called attention "to the fact that Uromyces Sophorae seems to possess a similar habit [that is, an intermingling of mycelia] to the perennial rusts under discussion." In any event, the presence of uredinia, in some cases at least, suffices to exclude this species from the short cycle forms.

UROMYCES PAVONIAE Arth., Bull. Torr. Bot. Club 31:1. 1914.—
Telospora Pavoniae Arth., Result. Sci. Congr. Bot. Vienne 346.
1906.

LITERATURE: SACCARDO, Syll. Fung. 17:250. 1905; Sydow, Monog. Ured. 1:59. 1909.

This rust, described upon Malache scabra B. Vogel (Pavonia racemosa L.) from Porto Rico and Jamaica, belongs with Puccinia

heterospora Berk. and Curt. An examination of the material shows that a very few 2-celled teliospores are present. P. heterospora, upon related Malvaceous plants, is characterized by the preponderance of 1-celled mesospores such as those upon Pavonia.

ARTHUR (Mycologia 9:80. 1917) has given a brief discussion of the situation here. Uromyces pictus Thuem. upon Abutilon was also found to possess a few 2-celled teliospores and was placed with Puccinia heterospora by Sydow (Monog. Ured. 2:58 and 356. 1910).

UROMYCES MONTANA Arth., Bot. Gaz. 39:386. 1905.—Telospora montana Arth., Result. Sci. Congr. Bot. Vienne 346. 1906.

The type collection of this species possessed also aecia, which were at the time considered to belong with *Uromyces Lupini* B. and C. Subsequent collections in Guatemala by Kellerman and Holway, however, show the same association of aecia and telia; furthermore, these aeciospores are larger and thicker walled than the aeciospores of *U. Lupini*. The grouped arrangement of the telia and the thin walls of the teliospores and their germination at maturity indicate a short cycle form, but nevertheless it is considered probable that the aecia go with the telia. *U. elatus* Syd., also upon *Lupinus*, shows the same situation as regards association of aecia with telia resembling those of a short cycle form. I am indebted to Dr. Mains of Purdue for work upon this species.

Uromyces Cupaniae Arth., Mem. Torr. Bot. Club 17:131. 1918.—Uredo cristata Speg., Anal. Soc. Ci. Argent 17:119. 1884.

This rust, although short-cycled, is excluded from this group, since, as noted by ARTHUR, it has marked affinities with other groups of rusts rather than with the group herein treated.

Conclusions

Eleven species of *Uromyces* possessing only telia and pycnia, or telia alone, are now considered to be present in North America. These are found especially in the higher and warmer portions of the continent, and occur upon 7 widely separated host families. While these rusts form a group agreeing as to life cycle and as to the 1-celled character of the teliospores, it is not considered that phylogenetic interrelationship is thereby shown, morphological evidence indicating rather that the relationship of a

species of these rusts is found in other rusts (of various life cycles and with 1 or 2-celled teliospores) upon the same or related hosts. Indeed, as indicated under *Uromyces heterodermus*, a group of hosts may bear a number of rusts of various life cycles, belonging to *Puccinia* and *Uromyces*, widely distributed geographically, yet all showing a certain unanimity of morphological characters, especially in the telial stage.

The writer wishes to express his keen appreciation to Dr. J. C. ARTHUR for suggesting this paper and for much help, and also to Professor Jackson for many suggestions and constructive criticism. To the other workers in the laboratory at Purdue University he is likewise greatly indebted.

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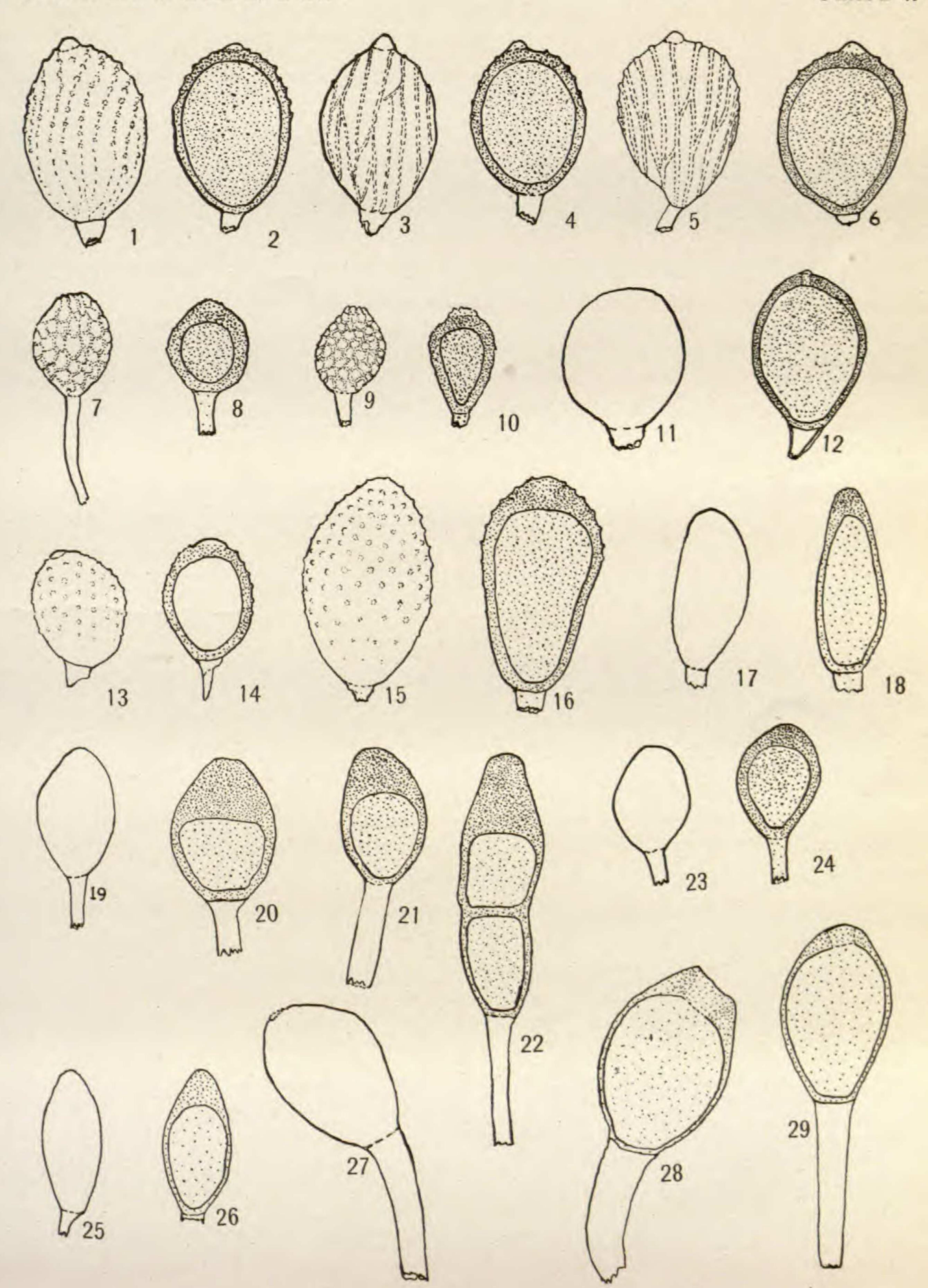
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EXPLANATION OF PLATE X

All figures were drawn at the level of the stage with the aid of a camera lucida, with Leitz 1/12 oil immersion and ocular 4. They are here reduced one-third, so that the magnification is 667 diameters. Surface markings, where present, are indicated, and the stippling on the optical cross-section diagrams



BISBY on UROMYCES